PANAMJAS
Pan-American Journal of Aquatic Sciences

Community structure and height distribution of intertidal rockpool fish in Los Cóbanos, El Salvador

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Abstract: Tide cycles determine the ecological complexity and environmental dynamics observed in the intertidal habitats. Intertidal dwellers show particular patterns of distribution with abrupt changes even at distances of few meters. Tropical intertidal zones have seldom been studied; therefore the community structure and vertical distribution of the intertidal rockpool fish of Los Cóbanos was assessed. In the intertidal zone, a total of 18 rockpools were selected according to the shore height as low (3-39 cm), mid (40-75 cm) and high (76-110 cm), with 6 replicate rockpools per shore level. Physico-chemical variables (temperature, salinity, pH), substratum homogeneity (algal, sand and rock cover) and habitat complexity were measured and rockpools were sampled every three months for one year. Overall, the intertidal assemblage of rockpool fish was composed of 48 species and dominated in abundance and species richness by the families Gobiidae (4 species and 746 fish or 31.29%) and Pomacentridae (5 species, 546 fish or 22.90%). The most abundant species were *Bathygobius ramosus* (27.76%) and *Stegastes acapulcoensis* (11.07%). Juvenile fish (75%) were more abundant than adults and larvae. Opportunist fishes were more abundant than permanent residents and transients comprising 58.53%, 39.87% and 1.6% of the abundance, respectively. Intertidal height, volume and rock cover were the most important variables that determined changes in the community structure. Six species presented size class segregation among rockpools at shore heights in the intertidal zone.

Key words: Intertidal rocky shore, fish community, rockpools, vertical zonation patterns

Resumen: Estructura comunitaria y distribución en altura de peces en piletas intermareales de Los Cóbanos, El Salvador. Los ciclos de marea determinan la complejidad ecológica y condiciones ambientales de los ambientes intermareales. Los organismos que habitan la zona intermareal muestran patrones de distribución con cambios abruptos aún a distancias de pocos metros. En los trópicos los estudios de las zonas intermareales son limitados; por lo que la estructura de la comunidad y a la distribución vertical de los peces en las pozas de la zona intermareal Los Cóbanos fue evaluada. En la zona intermareal 18 pozas fueron seleccionadas y clasificadas en tres niveles de acuerdo a su elevación en la plataforma intermareal como baja (3-39 cm), media (40-75 cm) y alta (76-110 cm) con 6 pozas por cada nivel. Las variables físico químicas (temperatura, salinidad, pH), homogeneidad del sustrato (cobertura de algas, arena o roca) y complejidad de hábitat fueron medidas en cada poza previo al muestreo realizado cada tres meses durante un año. El ensamblaje de peces intermareales estuvo conformado por 48 especies de peces y las familias que dominaron en riqueza y abundancia fueron Gobiidae (4 especies y 746 individuos o 31.29%) y Pomacentridae (5 especies, 546 individuos o 22.90%). Las especies más abundantes fueron *Bathygobius ramosus*

(27.76%) y *Stegastes acapulcoensis* (11.07%). Los peces jóvenes (75%) fueron más abundantes que adultos y larvas. Los peces oportunistas fueron más abundantes que los peces residentes y transitorios con un 58.53%, 39.87% y 1.6% de abundancia respectivamente. Las variables principales que determinaron los cambios en la comunidad de peces fueron la altura de la poza en la zona de marea, el volumen y el porcentaje de sustrato rocoso en las pozas. Seis especies de peces presentaron segregación de tamaños con peces pequeños o grandes utilizando elevaciones particulares en las pozas de la zona intermareal rocosa.

Palabras clave: zona intermareal rocosa, comunidad de peces, pozas de marea, patrones de zonación vertical

Introduction

The intertidal zone is a harsh and dynamic environment modified by the flooding and ebbing of tides. During the low tide, the water is retained in rockpools that experience less drastic environmental changes than the adjacent emergent substrata (Metaxas & Scheibling 1993). However, physical and chemical variables in rockpools are still very variable during low tide periods due to the shore height, with rockpools at lower levels on the shore experiencing less drastic changes than rockpools higher up on the shore (Daniel & Boyden 1975, Huggett & Griffiths 1986, Zander *et al*.1999, Hernández *et al*. 2002, Martins *et al*. 2007). Some of these environmental changes can be buffered, but not eliminated, by the volume of water in the rockpools (Daniel & Boyden 1975, Huggett &Griffiths 1986, Mahon & Mahon 1994, Cunha *et al*. 2008, Macieira & Joyeux 2011). For instance in temperate zones, the water temperature in rockpools in the high intertidal zone can be 15°C higher than those found in the low intertidal zone (Morris & Taylor 1983, Metaxas & Scheibling 1993), salinities can reach up to 40.0 PSU and pH up to 10 (Goss-Custard *et al*. 1979). These extreme variations challenge fish communities inhabiting intertidal rockpools.

Some fish species spend almost their entire life in the intertidal zone, whilst others visit intertidal habitats during a particular period of their life cycle, especially as juveniles, creating a diverse and dynamic community (Gibson & Yoshiyama 1999). Large-scale variations have been observed in the structure of intertidal assemblages with communities in temperate regions often composed mainly of a few species well adapted to the intertidal environment, whereas in the tropics, rockpools often support highly diverse communities due to the influence of subtidal species that visit rockpools as juveniles (Mahon & Mahon 1994, Gibson & Yoshiyama 1999, Cunha *et al.* 2007, Cunha *et al*. 2008, Macieira & Joyeux 2011). Intertidal fish that remain in rockpools have to cope with the abrupt environmental changes and show morphological, anatomical, physiological and behavioral adaptations that enable them to survive in this habitat (Berschick *et al.* 1987, Bridges 1988, Zander *et al.* 1999, Luck &Martin 1999, Ford *et al.* 2004). For example, many rockpool fishes have elongated bodies, pelvic fins modified to form a suck disk, reduced or absent swim bladder, are able to secrete mucus to avoid desiccation, reduced activity during harsh periods, small gill area, high density of cutaneous blood vessels and actively search for refuge during critical periods (Bridges 1988; Zander *et al.* 1999). However, these adaptations are not warranty for fish to use the whole range of rockpool habitats in the intertidal zone and spatial segregations among different stages of the life-cycle and among species have been observed in the intertidal zone (e.g. Yoshiyama 1981, Zander *et al*. 1999, Hernandez *et al.* 2002, Pulgar *et al.* 2005, Pulgar *et al*. 2007).

At the scale of the shore, spatial variation in environmental and biological variables among rockpools (i.e. in relation to rockpool location along the vertical gradient of shore height) can influence the abundance and distribution of many species (Gibson 1972, Yoshiyama 1981, Huggett & Griffiths 1986, Gibson &Yoshiyama 1999, Zander *et al*. 1999, Hernández *et al.* 2002, Griffiths *et al*. 2003, Martins *et al.* 2007). It is generally accepted that the species richness and abundance of the intertidal fishes gradually decrease from the low intertidal to the high intertidal shore (Yoshiyama 1981, Davis 2000b, Davis 2001, Castellanos-Galindo *et al.* 2005, Cunha *et al.* 2008,) because it is assumed that the physic-chemical stability of the rockpools determines the dynamic of the assemblage of fishes along the intertidal shore and rockpools in the low intertidal shore represent the most suitable habitat for fishes. Nevertheless there is a trade-off between the extreme locations in the intertidal shore. For instance Davis (2000b) and Almada & Faria (2004) proposed that pools lower in the intertidal zone undergo minor thermal and chemical changes because they are isolated for shorter periods of time

during low tide but are exposed longer time to predators of the subtidal zone. The rockpools in the high intertidal undergo drastic environmental changes and seems to be exposed to some terrestrial predators like aquatic birds (Yoshiyama 1981, Almada & Faria 2004). Therefore it is sensible to consider that the area in the mid intertidal could support a higher diversity because it represents intermediate conditions between both extremes of the intertidal shore in biological and environmental traits. Griffiths *et al.* (2003) studied the vertical distribution of the fish assemblages and concluded that the intermediate level of the rocky intertidal zone presented the highest diversity because it represented an area of overlap and the upper and lower limit of species restricted to the low and high intertidal zone respectively.

Intertidal dynamics can also affect abundance and length frequency distribution of the interidal fishes (Davis 2000b, Griffiths *et al.* 2003, Almada & Faria 2004). Gibson (1972) described fish distribution and abundance patterns in rockpools off the coast of France. Some species, for example, the shanny *Blennius pholis* (Linnaeus 1758)**,** occupied all positions along the vertical distribution of the intertidal zone, yet the abundance of the shanny varied in relation to shore height. Other species such as the Montagu's blenny *Coryphoblennius galerita* (Linnaeus 1758) and the giant goby *Gobius cobitis* (Pallas 1814) are limited to the upper part of the shore, whilst the rock goby *Gobius paganellus* (Linnaeus 1758) is limited to the lower parts of the shore. Furthermore, Yoshiyama (1981) documented that larger individuals of the fluffy sculpin *Oligocottus snyderi* (Greeley 1898) and the woolly sculpin *Clinocottus analis* (Girard 1858) were present in lower-shore pools in California and that their average size decreased toward rockpools higher on the shore. In addition, Hernández *et al.* (2002) tested whether differences in temperature tolerance could explain variations in the distribution of different size classes of the vieja *Graus nigra* (Philippi 1887) in intertidal rockpools of Chile, and concluded that physiological stress caused by water temperature restricted adult fish to rockpools lower on the shore and young fish to higher rockpools. The size of the fishes is also considered important during agonistic interactions at intra and interspecific level (Faria & Almada 2006; Faria & Almada 2001). Davis (2000b) reported that habitat partitioning in size has occurred in three species *Clinocottus analis, Girella nigricans*, and *Gobiesox rhessodon* with smaller fishes concentrated in high intertidal rockpools. These studies considered the importance of environmental factors, and the role that predation, competition and agonistic behavior within and between species could play in the generation of use of the habitat by fish of different sizes.

Community structure of intertidal fish has been widely studied along the American Pacific Coast with more emphasis on temperate (Yoshiyama 1981, Moring 1986, Varas & Ojeda 1990, Stepien *et al*. 1991, Pfister 1996, Polivdka & Chotkowski 1998, Davis 2000a,b, Ruiz-Camps *et al*. 2010) than on tropical latitudes (but see Weaver 1970, Castellanos-Galindo *et al.* 2005, Castellanos-Galindo & Giraldo 2008, Ruiz-Campos *et al.* 2010). In El Salvador, records of intertidal fish are incipient (González-Murcia & Marín 2011, González-Murcia *et al*. 2012). As a result, the objectives of this study were (1) to describe the assemblage structure of intertidal rockpool fish in Los Cóbanos, (2) to determine patterns of vertical distribution of intertidal rockpool fish, (3) to determine physical and chemical variables associated with rockpool fish and (4) to describe the size structure of intertidal rockpool fish according to rockpool shore height. We hypothesized that shore height influences patterns of distribution and abundance of the intertidal rockpool fish and predict that rockpool at mid intertidal shore heights will support greater diversity of fish, because it represents the area of overlap between low intertidal and high intertidal assemblages. We also predict that larger fish of resident species will occur in rockpools of the higher intertidal shore because they are well adapted to the intertidal environmental dynamics and that larger fish of opportunist species will be restricted to rockpools of the lower intertidal zone.

Materials and methods

Study area and sampling design: The intertidal assemblage of fish was investigated in 18 rockpools between July 2010 and April 2011 in the Area Natural Protegida Complejo Los Cóbanos rocky reef, 11km westward of Acajultla, Sonsonate, El Salvador (Fig. 1). During the study period tidal range varied between -26 to 218 cm. The quantity of rockpools in the area and their height on the shore were determined during low tide using a theodolite. Rockpools were classified by shore height as low (3-39cm), mid (40-75cm) and high (76-110cm) based on their elevation on the intertidal zone and no rockpool formations were present at levels higher than 1.10m. Six rockpools were randomly selected at each elevation and sampled on four occasions three months apart.

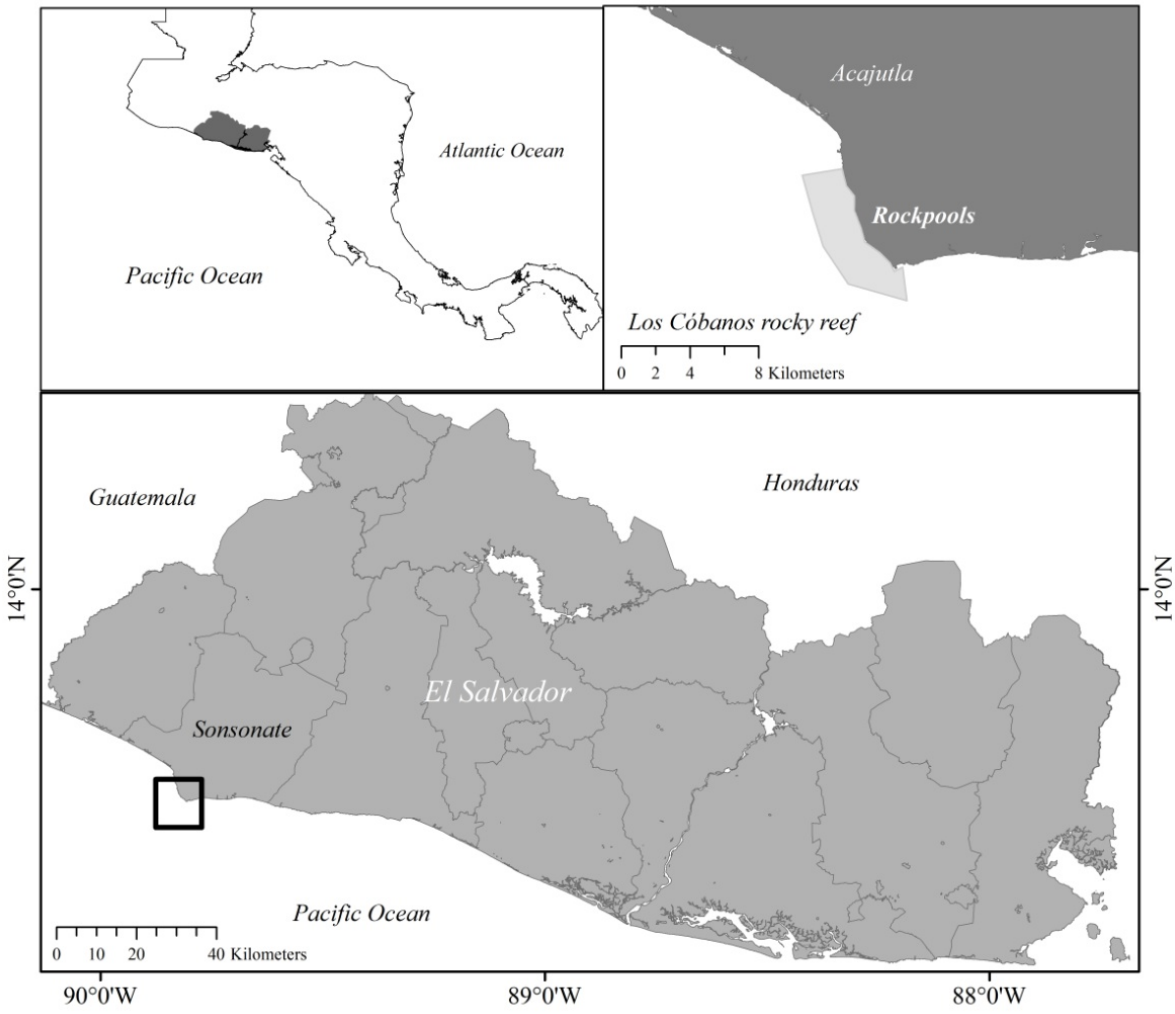

Figure 1. Location of the study area in the Marine Protected Area (MPA) Los Cóbanos, Acajutla, Sonsonate, El Salvador. Shaded area shows the location of the 18 sampled rockpools along the coast during July 2010 and April 2011.

Collection of rockpool environmental and structural data: Immediately before collecting fish, temperature (0.1°C), pH (0.1 pH units) and salinity were measured using a multi parameter HACH HQ40d. Volume was estimated by the formula V=A*D where V= is the rockpool volume, A= is the superficial area of the rockpool and D= is the average rockpool depth. The percent cover of algae, sand and rock was estimated using quadrats of 40x40cm (and 100 sub squares of 4x4 cm each mesh size) around the walls and bottom of each rockpool. Rockpool roughness was calculated by dividing linear distance between two points of the rockpool by the distance between the same points considering holes and crevices using a flexible tape. This gave a value between zero and one that indicated high and low roughness in the rockpools, respectively.

Fish assemblages: Rockpools were drained using a bilge water pump of 5.5 HP. Fish were collected using hand nets and by searching in crevices, algae and under rocks. Trapped fish were transferred to buckets and the total length of each individual measured to the nearest millimeter. Fish were released 30 m away from the sampled rockpool. Some voucher specimens were collected and preserved in 70% ethanol.

Each species was classified according to rockpool utilization following the criteria of Griffiths (2003): a**) Permanent Residents** (R); present as juveniles and adults in the intertidal zone with morphological, anatomical or physiological adaptations for this environment, b) **Opportunists (O)** usually found as juveniles that eventually migrate to subtidal zones, with few morphological adaptations for intertidal life and, c) **Transients (T)** which have no adaptations for intertidal life and usually get trapped in rockpools when the tide recedes.

Behavioral affinities of each species were categorized using the criteria established by Griffiths (2003) from qualitative observations in the field such as: a) **Solitary** (S), species which are normally observed alone or in pairs but not in schools, b) **Aggregating** (A), species that form schools or small congregations, c) **Cryptic** (C), species which possess camouflaged coloration and/or tend to be secretive by hiding in crevices, algae and under rocks and, d) **Territorial** (T), species which display aggressive behavior to defend a particular area.

Life history stages were arbitrarily determined by using the minimum length of post larval fish captured for each species with published records of maximum lengths and dividing the length range into three equal size classes to represent **juvenile**, **sub adult** and **adult**. However **sub adult** and **adult fishes** were pooled into the **adult** stage category. If fish presented sizes lower than the minimum length recorded for juveniles and absence of juvenile traits were categorized as **larvae**. We considered that this measure can provide an adequate indication of fish life history stages and has been successfully used in numerous studies of rockpool fishes (Grossman 1982, Lardner *et al.* 1993, Pfister 1996, 1997; Faria & Almada 1999, Ghanbarifardi & Malek 2009).

Finally, captured fish were preserved in 70% ethanol and samples were sent to the Museo de Historia Natural de El Salvador (MUHNES) and registered under catalogue number MUHNES 40-463 to 40-480. Some specimens were sent to the Collection of the Instituto de Ciencias del Mar y Limnología of the Universidad de El Salvador under the catalogue numbers ICMARES-UES 420 to ICMARES-UES 461. Many specimens (mainly Gobiesocidae) were sent to Philip A. Hastings of the Scripps Institution of Oceanography for taxonomic identification and then registered under catalogue number SIO-13-239 to SIO13-246.

Data analysis: The relationship between environmental variables and shore height was assessed using Spearman multiple range test (r_S). Abundance of individuals and species richness were standardized by rockpool volume and expressed as individuals or species per cubic meter (m^3) and log (x+1) transformed. Abundance and species richness of rockpool fish were compared among rockpools at different shore heights. However, because rockpool volume has been considered an important factor that influences the abundance and richness of fishes in rockpools (Mahon & Mahon 1994; Davis 2000b; Almada & Faria 2004; Cunha *et al.* 2007; Macieira & Joyeux 2011); the variable volume was included in the analysis as a covariate. Therefore, an Analysis of Covariance (ANCOVA) was performed using the model: abundance~height+volume+volume*height for abundance and in parallel way richness~height+volume+volume*height for species richness. When the interaction term was not statistically significant, it was removed from the model and the simplified model was: abundance~height+volume for abundance and in parallel way richness~height+volume for species richness. Due to the loss of some sample units in the mid intertidal as a product of seasonal sedimentation patterns in the intertidal zone, a type III sum of squares analyses was used to cope with the unbalanced design. If differences were detected in the factor variable a Tuckey- Kramer test was performed in order to detect the groups that were different. The samples were considered independent despite the same rockpools being sampled on each occasion, because the intervals between sampling events were long enough to allow complete re-colonization of rockpools (Lardner *et al*. 1993, Polivka & Chotkowski 1998, Faria & Almada 1999, Griffiths 2003; Griffiths *et al.* 2004).

Non-Metric Multidimensional Scaling (nMDS) analysis was used to examine similarities in fish assemblages among rockpool at different shore heights by using standardized abundances by volume of each species and square root transformation applied to construct a similarity matrix using the Bray–Curtis similarity coefficient (Clarke & Gorley 2006) in the PRIMER (Plymouth Routines in Multivariate Ecological Research) package. A one-way analysis of similarities (ANOSIM) was used to determine whether the structure of fish assemblages associated with the different rockpool heights varied statistically. This process involved generating 4999 random permutations of the data that were used to calculate the probability that observed differences in the structure of the fish assemblages could emerge by chance (Clarke & Gorley 2006). Similarity percentages (SIMPER) analysis was then used to determine which species of fish were responsible for significant differences among rockpools at different shore heights.

The relationship between fish community assemblage and environmental variables (temperature, salinity and pH) and structural variables (intertidal height, substrate homogeneity, algal, cover and rockpool volume) was evaluated using non-parametric multivariate analysis. A matrix of Euclidean distances was constructed for

environmental data and correlated with a similarly matrix constructed for fish assemblages based on a Bray-Curtis index. The process was performed with the BIOENV function of the PRIMER package using the Spearman correlation coefficient (ρ), to determine which combination of environmental variables best explained the relationship between both matrices.

Finally, the total length of the species whose abundance was larger than the 3% of the assemblage and that occurred in at least in 50% of the rockpools were compared among shore heights using a Kruskall-Wallis test to determine differences by intertidal rockpool height using the R statistics package. If differences were present, a Wilcoxon test was performed as a *post hoc* test. To correct for the inflation of type I error rates due to multiple testing, Bonferroni correction was applied and the significance level adopted was $p<0.016667$.

Results

Environmental data: Environmental variables varied among sampling events. Mean sea water temperature in rockpools ranged between 33.97 (±1.75 SD) °C in July 2010 and 31.18 (±1.17 SD)°C in January 2011. Salinity ranged from 31.18 (±3.36 SD) PSU in July 2010 to 34.90 (±1.15 SD) PSU in April 2011. The pH ranged from 8.60 (±0.16 SD) pH units in October 2010 to 8.21 (±0.24 SD) in April 2011 (Table I). Temperature and pH increased with intertidal height, but salinity did not vary with intertidal height (Table I.) Algal cover decreased with intertidal rockpool height whereas rock cover increased with intertidal height. Rockpool roughness and sand cover did not vary with intertidal height (Table I)

Table I. Environmental and habitat structure variables of the intertidal rockpools recorded in four sampling events from January 2010 to April 2011 and the relationship with the intertidal height tested with the Spearman´s rank test.

Variable	Sampling				Spearman´s Rank Test		
	1	2	3	4	ρ	p	n
Temperature °C	33.97±1.75	33.52±2.46	31.18±1.17	32.41±2.19	0.36	0.00*	61
Salinity PSU	31.18±3.36	32.60±1.76	32.6±5.01	34.9±1.15	0.13	0.28	61
pH	------	8.6±0.16	8.25±0.13	8.21±0.24	0.25	0.04*	61
Roughness LD/DR	0.87±0.07	0.87±0.06	0.89±0.06	0.87±0.08	-0.18	0.14	61
Algae %	9±17	11±16	18±17	14±15	-0.3	0.01*	61
Sand %	37±38	37±36	35±29	40±31	-0.22	0.08	61
Rocks %	50±38	53±34	36±23	44±33	0.29	0.02*	61

Fish composition: A total of 2,385 fish representing 48 species, 40 genera and 24 families were caught (Table II). Dominant families in terms of number of species were Pomacentridae (5 species), Gobiidae, Serranidae and Labridae (4 species per family). Dominant families in terms of numbers of individuals were Gobiidae (746 fish or 31.29%) and Pomacentridae (546 fish or 22.90%). The most abundant fish were the Panamic frillfin *Bathygobius ramosus* (Ginsburg 1947) (27.76%), the Acapulco major *Stegastes acapulcoensis* (Fowler 1944) (11.07%), the Pacific fat sleeper *Dormitator latifrons* (Richardson 1844) (10.36%), the Petaca *Abudefduf concolor* (Gill 1862) (9.85%), the Tinsel squirrelfish *Sargocentron suborbitale* (Gill 1863) (9.10%) and the Starry grouper *Epinephelus labriformis* (Jenyns 1840) (5.41%).

The structure of fish assemblage showed that opportunist fish were the most abundant group (1,396 individuals or 58.53%) followed by permanent residents (951 individuals or 39.87%) and transients (38 individuals or 1.6%). Juvenile fish were more abundant (1,803 individuals or 75.60%) than adults (315 individuals or 13.20%) and larvae (266 individuals or 11.20%) (Table II).

Assemblage structure: Species richness did not differ significantly among rockpools at different shore heights, but changes in species richness were related with the volume of the rockpools (Table III). Nonetheless, rockpools at mid and high shore levels of the intertidal zone tended to support, on average, a richer assemblage of fish than rockpools lower on the shore (Figure 2). The abundance of fish varied significantly among rockpool at different shore heights and with rockpool volume (Table III). Rockpools at mid and high shore levels of the intertidal zone supported greater abundances of fish than rockpools lower on the shore (Fig. 3) but significant differences were only detected among rockpools of the low and high intertidal shore (Tukey- Kramer $\alpha<0.05$).

Multivariate analysis (ANOSIM) showed that there significant differences among groups ($R=0.21$, $p= 0.013$) with *pair wise* comparisons revealing significant differences in the structure of fish assemblages between rockpools at low and mid

Table II. Abundance, life history stage, behavior affinity, residence category, total length (TL) and standard deviation (SD) of the intertidal fish assemblage of Los Cóbanos caught from January 2010 to April 2011. n= abundance, [b]Life history stage: A= adult, J=juvenile, L= larvae, [c]Behavior Affinity: S= solitary, C=cryptic, A=aggregating, T=territorial, [d]Residence status: R=Residents, O= Opportunist, T=Transients, [e]SD= standard deviation.

Family	Species	n[a]	Stage[b]	Behavior affinity[c]	Residence status[d]	Total length (mm)	Mean±SD[e]
Apogonidae	*Apogon dovii*	1	A	S	T	75	-----
Blennidae	*Ophioblennius clippertonensis*	8	J-A	S-C	O	59-95	77.87±14.89
Bothidae	*Engyophrys santilaurentii*	1	J	S	T	14	-----
Carangidae	*Caranx caninus*	3	J	S	O	59-70	66.00±6.08
Eleotridae	*Dormitaror latifrons*	247	L	A	T	10-20.1	12.30±1.05
Gerreidae	*Eucinostomus currani*	38	J	S-A	O	13-76	25.39±16.21
Gobiesocidae	*Gobiesox daedaleus*	101	J-A	S-C	R	12-50	29.63±8.11
Gobiesocidae	*Arcos rhodospilus*	1	J	S-C	R	30	-----
Gobiesocidae	*Tomicodon eos*	17	J-A	S-C	R	12-24	18.00±2.93
Gobiesocidae	*Tomicodon zebra*	13	J-A	S-C	R	13-25	18.69±3.14
Gobiesocidae	*Gobiesocidae.*	1	-----	S-C	R	14	-----
Gobiidae	*Bathygobius ramosus*	662	J-A	S-C-T	R	6-97	34.35±14.81
Gobiidae	*Gobionellus microdon*	19	L	G	R	15.3-16.6	15.82±0.28
Gobiidae	*Gobiosoma aceras*	1	J	S-C	R	39	-----
Gobiidae	*Gobiosoma paradoxum*	64	J	S-C	R	10-27	18.84±3.99
Grammistidae	*Rypticus bicolor*	4	J	S	O	21-70	55.25±20.90
Grammistidae	*Rypticus nigripinnis*	21	J	S	O	16-104	49.23±22.24
Holocentridae	*Sargocentron suborbitale*	217	J-A	S	O	42-130	75.96±19.43
Labridae	*Halichoeres chierchiae*	1	J	S	T	20	-----
Labridae	*Halichoeres dispilus*	1	J	S	T	74	-----
Labridae	*Halichoeres nicholsi*	33	J	S-A	O	10-60	22.21±14.93
Labridae	*Thalassoma lucassanum*	4	J	S	O	20-25	22.75±2.62
Labrisomidae	*Malacoctenus sudensis*	76	J-A	S-C	R	51-66	52.94±9.89
Labrisomidae	*Paraclinus beebi*	1	J	S-C	R	22	-----
Labrisomidae	*Paraclinus monophthalmus*	9	J-A	S-C	R	14-31	23.33±4.84
Lutjanidae	*Lutjanus argentiventris*	13	J	S	O	24-190	100.00±52.67
Lutjanidae	*Lutjanus colorado*	2	J	S	O	25-26	25.50±0.70
Lutjanidae	*Lutjanus jordani*	1	J	S	T	25	-----
Mugilidae	*Mugil curema*	89	J	S-G	O	30-94	64.48±17.37
Muraenidae	*Echidna nocturna*	25	J-A	S-C	R	132-650	292.44±139.32
Muraenidae	*Muraena lentiginosa*	1	J	S-C	R	206	-----
Nomeidae	*Psenes cyanophrys*	1	J	S	T	29	-----
Ophichthidae	*Myrichthys tigrinus*	3	J-A	S-C	O	20-35	266.66±17.37
Pomacanthidae	*Pomacathus zonipectus*	11	J	S	O	21-50	30.90±10.07
Pomacentridae	*Abudefduf concolor*	235	J	S-A	O	11-74	26.76±11.17
Pomacentridae	*Abudefduf troschelii*	39	J	S-A	O	19-76	36.84±14.70
Pomacentridae	*Microespathodon dorsalis*	2	J	S	O	50-70	60.00±14.14
Pomacentridae	*Stegastes acapulcoensis*	264	J-A	S-T	O	10-170	75.03±28.33
Pomacentridae	*Stegastes flavilatus*	6	J	S	O	15-50	30.00±11.45
Scaridae	*Nicholsina denticulata*	1	J	S	T	64	-----
Scorpaenidae	*Scorpaena mystes*	3	J	S-C	O	90-115	101.66±12.58
Serranidae	*Cephalopholis panamensis*	7	J	S	O	40-119	86.57±27.47
Serranidae	*Epinephelus analogus*	1	J	S	T	51	-----
Serranidae	*Epinephelus labriformis*	129	J	S	O	19-220	95.00±30.05
Serranidae	*Mycteroperca xenarcha*	1	J	S	T	25	-----
Syngnathidae	*Doryramphus excisus*	2	J-A	S	O	22-54	38.00±22.62
Tetradontidae	*Arothron hispidus*	2	J	S	O	19-81	50.00±43.84
Tetradontidae	*Arothron meleagris*	3	J	S	O	19-42	27.33±12.64

shore heights (R= 0.22, p= 0.030; Fig. 4) and between rockpools at low and high intertidal shore heights (R= 0.419, p= 0.002; Figure. 4).

SIMPER analysis demonstrated that heights

Table III. Results of the Analysis of Covariance (ANCOVA) with the species richness and abundance as dependent variables and shore height and volume as factor and covariate respectively.

Variable	df	Sum of Squares	Mean Squares	*F* value	P (F)
Species richness					
Volume	1	1.68858	1.688577	7.963035	0.0065611
Height	2	0.20511	0.102554	0.483626	0.6190504
Residuals	57	4.932414	0.086534		
Abundance					
Volume	1	5.70101	5.701009	13.73773	0.0004773
Height	2	2.99979	1.499897	3.61431	0.03327901
Residuals	57	12.08696	0.212052		

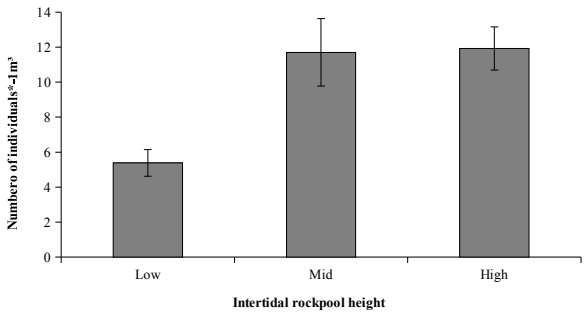

Figure 2. Mean (±SD) species richness of fish in the low (3-39cm), mid (40-75cm) and high (76-110cm) elevation on intertidal zone of Los Cóbanos, Acajutla El Salvador. Elaborated in Excel program

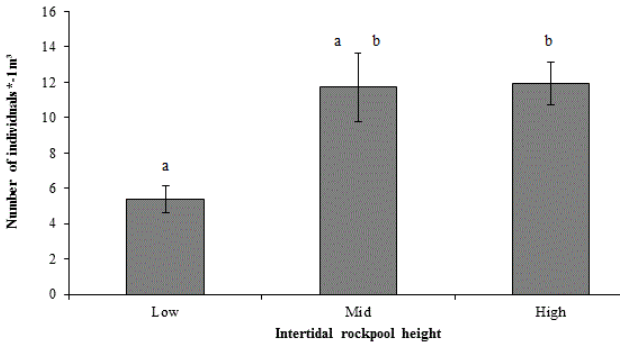

Figure 3. Mean (±SD) abundance of fish in the low (3-39cm), mid (40-75cm) and high (76-110cm) elevation on intertidal zone of Los Cóbanos, Acajutla El Salvador. Letters indicate the outcome of the Tuckey-Kramer test of all pair of means at $\alpha<0.05$.

were mostly influenced by *B. ramosus* (9.34%), *G. daedaleus sp1* (6.63%), *M. sudensis* (6.12%), *A. concolor* (5.46%) and *H. nicholsii* (5.06%) that presented higher abundances in the mid shore height and the lower abundance of *S. acapulcoensis* (7.41%) in the rockpools of the mid shore. These six species represented the 40.03% of the overall differences between the assemblages of the low and mid shore heights.

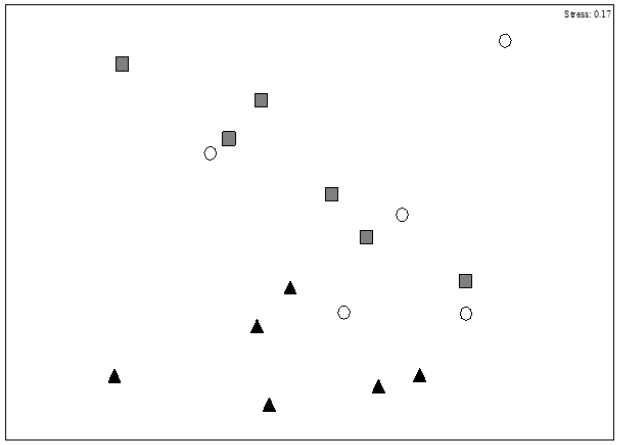

Figure 4. Non Metric Multidimensional Scaling (nMDS) representing fish assemblage structure in rockpools at low (▲), mid (○) and high (■) intertidal shore heights in Los Cóbanos based on the square root-transformed data and Bray-Curtis similarity index. Stress values are shown.

The differences in the structure of fish assemblage between rockpools at low and high intertidal shore heights were mostly influenced by *A. concolor* (10.27%), *B. ramosus* (9.74%), *S. suborbitale* (8.05%), Paradox goby *Gobiosoma paradoxum* (Günther 1861) (6.57%), White mullet *Mugil curema* (Valenciennes 1836) (6.29%) and *M. sudensis*(5.42%) that presented higher abundances in the rockpools of the high shore height and *S. acapulcoensis* (7.41%) that presented lower abundances in the rockpools of the high shore. These seven species represented 56.05% of the overall difference between the fish assemblages of the rockpools of these shore heights.

The differences in the structure of fish assemblage between rockpools at mid and high intertidal shore heights were mostly influenced by *S. acapulcoensis* (8.87%), *G. daedaleus* (7.93%), *A. concolor* (6.64%), *S. suborbitale* (6.86%), *G. paradoxum* (5.92%) and *M. curema* (5.51%) that presented higher abundances in the rockpools of the

high shore height and *Bathygobius ramosus* (7.96%), *M. sudensis* (7.47%) that presented lower abundances in the rockpools of the high shore. These seven species represented 57.15% of the overall difference between the assemblages of the rockpools of these shore heights. The BIOENV analysis showed that the arrangement of variables that best explained the changes of the fish assemblage in the intertidal shore were height, volume and rock cover (ρ =0.285).

Length structure: Total length of the resident fish *B. ramosus* (662), *G. daedaleus* (95), and *G. paradoxum* (Günther, 1861) (64) and transient fish *S. suborbitalis* (217), *S. acapulcoensis* (264), *E. labriformis* (129*), A. concolor* (235) and *M. curema* (89) varied significantly with rockpool height on the shore (Figure 5 and Table IV). The three resident species *B. ramosus*, *G. daedaleus*, and *G. paradoxum* and the opportunist *A. concolor* presented the same trend with smaller fish in rockpools of the low intertidal shore and larger fish in rockpools of the high intertidal shore. The larger fish of the opportunist species *S. suborbitale* and *S. acapulcoensis* inhabited the rockpools of the mid shore height. Finally the opportunist *E. labriformis* presented a trend with larger fish in rockpools of the low intertidal shore and smaller fish in rockpools of the high intertidal shore (Figure 5 and Table IV).

Discussion

The families Gobiidae and Pomacentridae were dominant in abundance and species richness in Los Cóbanos. The dominance of Gobiidae and Pomacentridae in terms of abundance and species richness has been reported in the Tropical Eastern Pacific (TEP) intertidal rockpools of Colombia (Castellanos-Galindo *et al*. 2005), Costa Rica (Weaver 1970) and El Salvador (González-Murcia *et al.* 2012) and the only exception to this pattern in the TEP is presented by Ruiz-Campos *et al*. (2010), where Cottidae and Blennidae were dominant. However, it differs with patterns recorded in temperate latitudes of the Pacific coast of America, in which dominant families in terms of abundance and species richness are members of the families Cottidae, Sticheidae, Blennidae, Gobiesosidae and Labrisomidae (Yoshiyama 1981, Moring 1986, Varas & Ojeda 1990, Muñoz & Ojeda 1997, Davis 2000a, b, Berrios & Vargas 2004). Members of the last three families, were present in the intertidal zone of Los Cobanos and are well adapted to tolerate the harsh conditions of this environment (Horn *et al.* 1999), the overall low abundance and species richness in the intertidal zone could be determined for other ecological factors that exert effects at local scales like competition, low availability of habitats and predation. On the other hand, Pomacentridae had high species richness with 34 endemic species in the Tropical Eastern Pacific (TEP) and high abundance in rocky reef ecosystems (Robertson & Allen 2015). Additionally juvenile stages have been reported in high abundances in TEP intertidal rockpools habitats (Castellanos-Galindo *et al*. 2005, Castellanos-Galindo & Giraldo 2008). Thus, intertidal rockpool icthyofauna in Los Cóbanos is dominated in abundance and species richness by a set of species that seems to be particular for the intertidal rockpools of the TEP.

The intertidal rockpool assemblage recorded in Los Cóbanos is the second most diverse intertidal habitat described in the TEP. The 24 families and 48 species recorded in this study is lower than recorded by Weaver (1970) on the Pacific coast of Costa Rica with 25 families and 60 species, similar to the study by Ruiz-Campos *et al*. (2010) with 48 species and 20 families and higher than claimed by Stepien *et al*. (1991) with 19 species and seven families and by Castellanos-Galindo *et al.* (2005) on Isla Palma, Colombia with 12 families and 14 species. Disparities in species richness with the assemblage reported by Weaver (1970) could be the result of differences in spatial sampling effort that included many rockpools formations along the Costa Rica coast, higher habitat diversity with rockpools located nearby rocky reefs and estuaries that allowed the occurrence of estuarine and freshwater fish, and rockpool volume differences that were greater than the rockpools sampled in this study (0.01-23.1m^3). Differences with the assemblage described by Ruiz-Campos *et al.* (2010) are attributed to a higher sampling effort due to this study covered from the 32˚10'N to the 23˚20'N in the Baja California Peninsula. On the other hand, differences with the assemblage recorded by Castellanos-Galindo *et al.* (2005) in Colombia could be caused by lower sampling effort and smaller rockpool volume (0.087–1.35m^3) than the rockpools in this study. The extent to which biogeographical patterns influence these differences is difficult to quantify, but it is evident that the assemblages described by Ruiz-Campos *et al*. (2010) and Stepien *et al.* (1991) have different species composition. Finally, the effect of rockpool volume is supported by Cunha *et al*. (2007) and Mahon & Mahon (1994), who concluded that rockpool volume is related to increases in species richness in rockpool habitats.

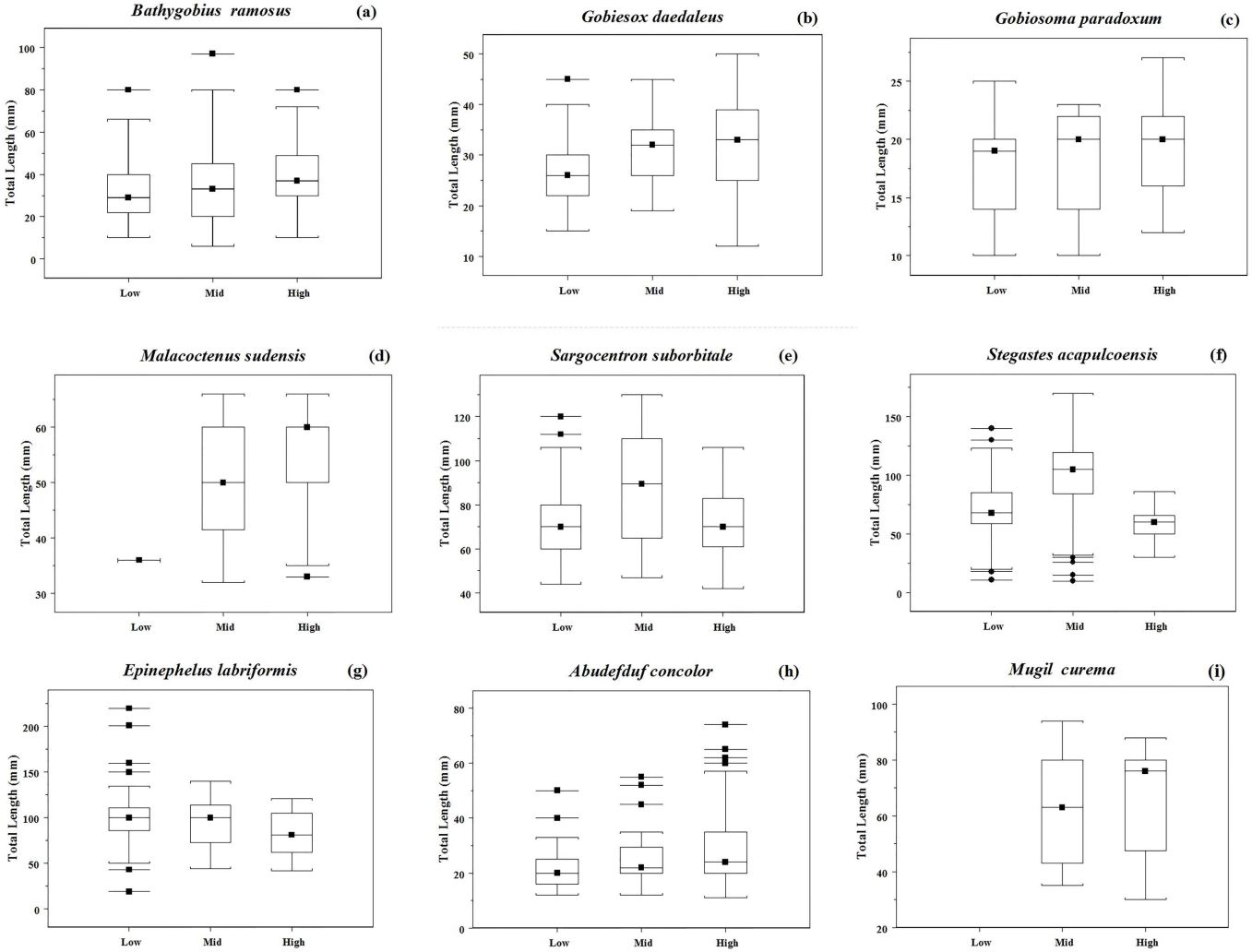

Figure 5. Total length (mm) distribution of *Bathygonius ramosus* (a), *Gobiesox daedaleus* (b), *Gobiosoma paradoxum* (c), *Malacoctenus sudensis* (d), *Sargocentron suborbitale* (e), *Stegastes acapulcoensis* (f), *Epinephelus labriformis* (g), *Abudefduf concolor* (h) and *Mugil curema* (i) in the low intertidal (Low: 3-39cm), mid intertidal (Mid: 40-75 cm) and high intertidal (High:75-110 cm) rockpools of Los Cóbanos, El Salvador.

Table IV. Range and median (mm) in low, mid and high rockpools of the nine most abundant fish and results of Kruskall-Wallis test and *post hoc* Wilcox test between low and mid, low and high and mid and high lengths of fish. *p<0.05; **p<0.01;***p<0.001.Bonferrani correction factor was applied and p<0.016667 was used as critical value to compensate for multiple test over the data during the pair comparisons with the Wilcox test.

Species	Low		Mid		High		Kruskall-Wallis test			Wilcox test					
	Range (mm)	Median	Range (mm)	Median	Range (mm)	Median	Value	df	p	Low-Med		Low-High		Mid –High	
										W	p	W	p	W	p
Bathygobius ramosus	10-80	29	6-97	33	10-80	37	33.52	2	0.000***	22404	0.133	17796.5	0.000***	17949	0.001***
Gobiesox daedaleus	15-45	26	19-45	32	12-45	31	9.18	2	0.010**	151.5	0.049	526	0.004**	273	0.7226
Malacoctenus sudensis	36	36	32-66	50	33-66	60	6.36	2	0.041*	4	0.224	2	0.129	496	0.038
Gobiosoma paradoxum	10-25	19	10-23	20	12-27	20	1.05	2	0.5893	-----	-----	-----	-----	-----	-----
Sargocentron suborbitale	44-120	70	47-130	89.5	42-106	70	14.17	2	0.000***	1957	0.000***	2824	0.766	2188.5	0.002**
Stegastes acapulcoensis	11-140	68	10-170	105	30-86	60	55.60	2	0.000***	2347	0.000***	5353	0.000***	2835	0.000***
Abudefduf concolor	12-50	20	12-55	22	11-74	24	15.01	2	0.000***	830	0.104	1632.5	0.000***	3161.5	0.024
Epinephelus labriformis	19-220	100	44-140	100	42-121	81	7.03	2	0.029*	1135	0.891	1283	0.008**	715	0.048
Mugil curema	-----	-----	35-94	63	30-88	76	1.22	1	0.268	-----	-----	-----	-----	-----	-----

Juvenile fish represent 75% of the rockpool intertidal assemblage in Los Cóbanos. The occurrence of a high number of juvenile fish is a frequent pattern on tropical and temperate intertidal rockpools worldwide and for this reason rockpools have been suggested as a nursery area (Moring 1986, Yoshiyama *et al*. 1986, Varas & Ojeda 1990, Lardner *et al*. 1993, Mahon & Mahon 1994, Pfister 1996, Quijada 2000, Griffiths 2003, Barreiros *et al*. 2004, Castellanos-Galindo *et al*. 2005, Faria & Almada 2006, Cunha *et al.* 2007, Ghanbarifardi & Malek 2009). Additionally, it has been proposed that rockpools are advantageous sites for survivorship during early stages and serve as a refuge during low tide especially for transient fish that could contribute a high number of individuals to adult stocks and shape the structure of subtidal assemblages (Mahon &Mahon 1994, Horn *et al*. 1999, Cunha *et al.* 2007). However, to accurately determine that a habitat is a nursery site, juvenile fish density is not enough and traits such as growth, survival and recruitment rates for adult populations should be evaluated for the habitats in which juvenile fish occur; and the effects of scale, resources, processes, complexity and connectivity in ecosystems and reproductive value of a nursery ground should be considered (Beck *et al*. 2001, Dahlgren *et al.* 2006, Sheaves *et al.* 2006). Indeed, intertidal rockpools in Los Cóbanos have high densities of juvenile fish, however to unequivocally establish the role of this habitat as a nursery, further research is required.

Changes in abundance and species richness in the intertidal fish community of Los Cóbanos were related with differences of height, volume and rock cover of the rockpools. The influence of height and volume of rockpools on intertidal icthyofauna has received attention to some extent, producing diverse results (Gibson 1972, Daniel & Boyden 1975, Huggett &Griffiths 1986, Griffiths *et al*. 2003, Castellanos-Galindo *et al.* 2005, Cunha *et al.* 2007). The increase in species richness with rockpool volume has been proved by Cunha *et al*. (2007) and Mahon & Mahon (1994) in the Tropical Atlantic Coast of America. In the TEP Castellanos-Galindo *et al.* (2005) did not find a relationship between intertidal diversity and volume, but reported that species richness decreased with height. These results contrast with the pattern observed in the present study, in which species richness was related with rockpool volume and the abundance changed significantly with height. Nonetheless, it is important to consider that variation in tidal amplitude and rockpool location make accurate comparisons between sites difficult. For instance, rockpools in Los Cóbanos were between 3 and 110 cm high with no rockpools above this level and a tidal range between -26 to 218 cm. On the other hand, Castellanos-Galindo *et al*. (2005) described the dynamics of rockpools 55 to 240 cm high in a 400 cm tidal range. Probably, patterns observed in the present study describe a narrow frame of the dynamics present in low rockpools described by Castellanos-Galindo *et al*. (2005) and lack of representation of the dynamic of these habitats in upper levels. Particularly relevant is the role of rock cover that could have created more diverse microhabitat to support higher abundance and species richness. For example, Almada & Faria (2004) considered that microtopography of rocks can provide refuges to particular species modifying their abundance and that the availability of sites determines the particular structure of the community in a rockpool. Certainly, height, volume and rock cover play an important role in the dynamics of Los Cóbanos rockpools, even in this narrow range of tides, in which sharp and detailed changes in the community have been observed, showing that the fish community tends to respond to local conditions that can present slight variation in the intertidal zone. Therefore in future rockpool studies in Los Cóbanos, variables such as height, volume and rock cover must be taken into account due to their influence in the intertidal icthyofauna.

Many environmental variables present concomitant changes with rockpool, volume and height (Daniel & Boyden 1975, Huggett & Griffiths 1986, Metaxas & Scheibling 1993, Mahon & Mahon 1994, Horn *et al*. 1999, Hernández *et al*. 2002, Castellanos-Galindo *et al*. 2005, Cunha *et al*. 2007) generating diverse microhabitats that affect distribution between species and within species. Abundance and species richness were greatest in the mid intertidal of rockpools. Griffiths *et al*. (2003) described a similar pattern and suggested it could be the result of the overlap of species from the high and low intertidal at this level. This is a plausible explanation considering that variables like temperature, pH, algal and rock cover were related to height generating higher diversity of habitats in this height; and environmental conditions with intermediate variation in comparison to low and high levels. Despite rockpools in the high level being exposed for longer periods during low tide, these rockpools had high abundances and species richness of resident species *G. daedaleus* and *G. paradoxum* and opportunists like *S. acapulcoensis, A. concolor,*

S. suborbitale and *M. curema.* It demonstrates that not only resident species with morphological and anatomical adaptations are able to cope with the harsh environment of the intertidal zone, but also opportunist fish that probably rely more on behavioral or physiological adaptations that allow them to survive during low tide when drastic environmental changes occur. The low abundance and richness detected in rockpools of the low intertidal, which theoretically have more favorable environmental conditions, could be the result of biological factors. Thus, the patterns of distribution observed in Los Cóbanos need to include environmental and biological factors that could act in synergy to determine particular distribution aspects of the intertidal fish assemblage.

Disparities observed in size classes and abundance patterns of residents *B. ramosus, G. daedaleus* and opportunists *A. concolor E. labriformis, S. suborbitale* and *S. acapulcoencis* open the gate for multiple ecological explanations. First, it could be considered that these arrangements are result of physiological constraints and agonistic interactions. For example Hernández *et al*. (2002) showed that smaller individuals (8.9-13.4cm) of the opportunist fish *Graus nigra* are more capable of tolerating drastic environmental changes during low tide than larger fish (17.9-22.4 cm) and that large *G. nigra* displayed aggressive behavior against smaller conspecifics displacing them to unsuitable areas. The role of agonistic interactions has been documented in members of the family Pomacentridae by Robertson (1996) and intertidal rockpools (Faria & Almada 2001). Second, it could be possible that larger individuals agglomerate in more suitable habitats displacing smaller fish to areas with higher predation. This is supported by the presence of large individuals of *E. labriformis* in the low intertidal. *Epinephelus labriformis* is a carnivorous fish that consumes crustaceans and small fish (Aburto-Oropeza *et al*. 2008) and could have consumed smaller individuals of other species in the low intertidal. Additionally, low intertidal rockpools could be exposed for longer period of time to predators from the subtidal zone as has been hypothesized by Yoshiyama (1981). Third, the length distribution and abundance could have been affected by the arrival of new recruits to specific areas in the intertidal as has been suggested by Davis (2000b). Future field and laboratory experiments are necessary to unequivocally determine the importance of physiological or biological features in the patterns of abundance and size classes observed.

This study contributes towards filling the knowledge gap in the rockpool fish communities in the TEP and explores some important points of the intertidal community. Los Cóbanos stands as one of the most diverse intertidal fish assemblages in the TEP dominated in abundance and species richness for the families Gobiidae and Pomacentridae. Age structure of the community shows that a high number of juvenile fish occur in this habitat and that fish can be potentially classified as resident, opportunist and transients based on the use of the rockpool. Vertical distribution of fish assemblages is mainly affected by three variables height, volume and rock cover and the highest diversity is present in the mid intertidal between 40-75 cm. Segregation in abundance and size classes of the fish is present, but factors generating these patterns must be tested.

Acknowledgements

To A. Anzora for his help in determining rockpools heights, to C. Marín, S. Grimaldi, S. Álvarez, E. Cornejo, V. Pereira, X. Pocasangre and J. González who helped during field sampling, A. María Velázquez, W. Morán and Wilfredo from FUNDARRECIFE for field assistance, to R. Esquivel for allowing the use of laboratory facilities, to P. Hastings for taxonomic identification of fish, to Colón City Hall for research funding and to S. Gonzalez Rosales and M. Murcia Orellana for their support.

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Received: February 2016
Accepted: August 2016
Published: October 2016